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# The effects of rainfall on plant–pollinator interactions

David A. Lawson<sup>1</sup> · Sean A. Rands<sup>1</sup>

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## Abstract

As global surface temperatures rise, global precipitation rates are predicted to increase. These localised increases in rainfall patterns may significantly affect plant–pollinator interactions in multiple ways. Detrimental effects to plant–pollinator interactions could have significant ecological and economic consequences, and so it is important to understand the effects that rain has on these mutualisms. Increased rainfall has the potential for population-level effects but there also wide scope for individual-level effects, which have received surprisingly little attention. Changes in rainfall patterns could alter the timings of phenological phases while also increasing the likelihood of pollen degradation and nectar dilution, each having detrimental effects to the fitness of the plant, the pollinator or both parties. Pollinators could also be affected through mechanical and energetic constraints, along with disruption of foraging patterns and disruption to sensory signals. In this review, we demonstrate that there are clear gaps in our knowledge of these events, the exploration of which should open new areas of debate surrounding the effects of climate change on biological systems.

**Keywords** Rainfall · Climate change · Plant–pollinator interaction · Nectar dilution

## Introduction

Environmental conditions have a critical impact on the relationship between plants and pollinators. Seasonality plays a crucial role, acting as a large-scale driver of environmental conditions (Memmott et al. 2007); however, local environmental conditions that occur within seasons also affect plants and their pollinators. Rainfall is one such environmental effect that has the potential to affect plant–pollinator interactions, as rain could have direct physical effects on both flowers and their pollinators, as well as interfering with the timing of pollinator visitations. A report by the Intergovernmental Panel on Climate Change states that it is a ‘virtual certainty’ that as mean global surface temperatures rise, global precipitation will also increase (Collins et al. 2013), with an ongoing trend for precipitation to fall as rain rather than snow in certain regions (Knowles et al. 2006). More recent climate projections also suggest an increase in

heavy precipitation in many high-elevation and high-latitude regions if temperatures continue to rise (IPCC 2018). In light of these localised increases in rainfall, it is important that we understand the effects this will have, both detrimental and beneficial, on plant–pollinator interactions, which hold major ecological and economic significance (Crepet 1984; Dodd et al. 1999; Klein et al. 2007; Gallai et al. 2009; Vamosi and Vamosi 2010).

The increasing availability of rainfall data has allowed for the development of computational models which estimate changes in global precipitation, which includes rain, snow, sleet and hail (Gehne et al. 2016). However, these estimates differ greatly due differences in calculation methods, precipitation measurement products and the goals for producing the estimates (Gehne et al. 2016). It is expected that there will be substantial spatial variation in these changes, with some regions experiencing increases in rainfall and others decreases, but high-latitude land masses are likely to experience greater amounts of precipitation along with tropical regions (Collins et al. 2013). For instance, winter rainfall is projected to increase across north central and western Europe (Scaife et al. 2012).

The prospect of increases in localised rainfall is made more troubling when coupled with the fact that pollinator diversity and abundance is in decline at a global scale

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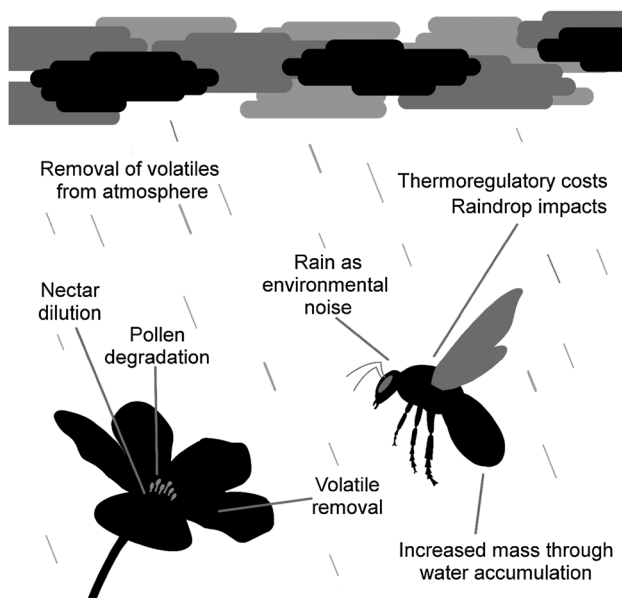
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✉ David A. Lawson  
david.lawson@bristol.ac.uk

<sup>1</sup> School of Biological Sciences, University of Bristol,  
BS8 1TQ Bristol, UK

(Biesmeijer 2006; Potts et al. 2010; Lebuhn et al. 2013) due to anthropogenic pressures such as land-use intensification, climate change, introduction of invasive species and disease (Rathcke and Jules 1993; Brown et al. 2002; Ghazoul 2004; Brown and Paxton 2009). With these projected climatic changes in mind, alongside the increasing risks pollinators face, it is crucial to gain a deeper understanding of how rainfall affects plant–pollinator interactions. Although rain often occurs along with a suite of other environmental conditions, such as increases in wind speed and decreases in temperature and light intensity, we will focus in this review on the different ways in which the process of pollination can be affected by rainfall specifically, as summarised in Fig. 1. The review will focus on pollen degradation, floral architecture, corolla closure, nectar dilution, flight mechanics, pollinator morphology, rain avoidance and energetics of flight during rain. This review also focusses on the presence and effects of rain at an individual level rather than the effects of increased or decreased water availability, and for this reason, species distributions and the temporal disruption of phenological phases will not be discussed. We call attention to gaps in our knowledge and highlighting avenues for future research, with the hope that this review will motivate new research in the area.



**Fig. 1** Diagram summarising the effects of rainfall on both flowers and pollinators

## Effects on plants

### Threats to flower—pollen degradation, floral architecture and corolla closure

Biotic pollination relies on the successful transfer of pollen from one flower to another, enabling sexual reproduction in plants. Rain can disrupt this pollen transfer and therefore hinder the reproductive efforts of flowering plants through several mechanisms. For many plants, contact with free water renders pollen grains inviable through osmotic disruption, interfering with this pollen transfer and causing a significant reproductive disadvantage to the plant (Corbet and Plumridge 1985; Jacquemart 1996; Burke 2002; Huang et al. 2002; Sun et al. 2008), with rain being a potential cause of this water contact (Akamine and Girolami 1959). However, this pollen degradation through water contact does not occur in all plant species (Eisikowitch and Woodell 1974; Huang et al. 2001). Some plant species utilise rain for self-pollination (Hagerup 1950; Fan et al. 2012), and it has been suggested that certain species could disperse pollen to other flowers through the action of rainfall (Hagerup 1950; Brodie 1954) as is seen for seed dispersal (Amador et al. 2012). It has also been suggested that rainfall which occurs before pollination can compromise the adhesion of pollen to the stigma surface of flowers (Akamine and Girolami 1959; Ortega et al. 2007), meaning rain has the potential to impair both male and female reproduction in flowering plants.

Plants mitigate these detrimental effects in a number of ways. A study of 86 selected angiosperm species found that 29 species presented pollen in the rain (Percival 1955). Of these 29 species, 12 had partial protection from rainfall from flower positioning or foliage and three species had complete protection due to the corolla form (Percival 1955). Further studies which examined flower structures and rain-susceptibility of pollen in 80 flowering species also found that the pollen of most species was susceptible to damage by water, implying that rain may directly reduce the fertility of unprotected pollen (Mao and Huang 2009). In the same study, it was found that in species where the pollen was completely protected by flower structure there was a low resistance to water, whereas in species with structures that did not protect pollen from rain there was a higher frequency of water-resistant pollen. These findings support the hypothesis that floral structures protect susceptible pollen during rain and that rain acts as a selective force shaping floral form which mirrors previous studies where flower structures were suggested to protect pollen in species that were susceptible to damage by rain (Dafni 1996; Aronne et al. 2006). Mao and Huang (2009) also note that understanding plant reproductive strategies for protecting pollen from rain may provide a clue to the diversity of plant–pollinator interactions.

These partial or complete protective structures can be an ever-present feature of the floral architecture (Sun et al. 2008; Mao and Huang 2009), or can be temporally induced through bending of flower stalks during anthesis which changes the orientation of the flower (Huang et al. 2002) and through closure of the corolla (Bynum and Smith 2001). In environments where there is a risk of rain damage, the protection afforded by these structures allows for prolonged anthesis, which benefits the reproductive success of the plant, particularly benefitting those species that have long floral life spans with relatively low visitation rates (Ashman and Schoen 1994; Sun et al. 2008).

In addition to these structures, hydrophobic floral surfaces and gradual presentation of pollen may mitigate this pollen damage (Percival 1955; Tadey and Aizen 2001; Whitney et al. 2011). Genera with down-facing flowers increase along a precipitation gradient in the Southern South American Andes (Aizen 2003), suggesting rainfall is a strong selective agent for down-facing flower orientation. However, the rain protection benefits of downward-facing flower orientation could not be confirmed in certain species which were more closely investigated (Tadey and Aizen 2001). This highlights the need to explore the function of these adaptations in more species and how they relate to other aspects of floral architecture such as the epidermal structure (Rands et al. 2011). Considering this potential for pollen damage, and the varying sensitivities of different plant species, more experimental research investigating which plants are more susceptible to pollen damage through rainfall would be beneficial to recognise which populations may be at greater risk in the future.

As storm tracks are also predicted to shift, with an overall increase in storm events and their intensity over time as temperatures rise (Collins et al. 2013), many flowering plants will experience an increase in storm exposure. This increased exposure to intense rainfall during storms may leave many plants vulnerable to physical damage (Jackson 1978; Pacini 1984) and increase the number of diseased flowers in some species (Beatley 1974). However, little is known about these effects. In light of this knowledge gap, it would be beneficial to further understand the risks posed to flowers during these events.

## Nectar dilution

Flowers which are exposed to rain also risk dilution of their nectar reserves. Nectar is the primary floral reward for the majority of pollinators and consists of sucrose, glucose and fructose dissolved in water, amongst other trace materials (Baker and Baker 1983). Nectar varies in concentration from around 7–70% sugar, with this concentration varying to some degree day-to-day and hour-to-hour due to changes in humidity (Butler 1945). In insect pollinators, this ingestion of nectar generally occurs through

the use of a proboscis which facilitates lapping or suction (Krenn et al. 2005) but can also utilise capillary action (Monaenkova et al. 2011). Differences in concentration, composition, viscosity and abundance are associated with different plant phylogenies and different pollinators (Nicolson 1998), with evidence that concentration is the primary discrimination factor in terms of pollinator choice, even when total energy profits of the choices are approximately equal (Butler 1945; Cnaani et al. 2006).

Bee-pollinated flowers usually have high sugar concentrations, whereas flowers pollinated by butterflies, moths and hummingbirds have more dilute nectars (Pyke and Waser 1981; Baker and Baker 1983). These associations are thought to relate to the requirements of pollinators, such as the speeds at which pollinators can ingest nectar at certain concentrations and specialised digestive constraints (Heyneman 1983; Martinez del Rio et al. 1992). However, there appear to be no clear-cut associations for nectar concentrations, compositions and pollinators in the temperate forest of southern South America, and even differences between populations of the same species (Chalcoff et al. 2006), suggesting there is more to be explored in this area.

Rainfall has the potential to dilute nectar (Butler 1945; Eisikowitch and Woodell 1975) and diluted nectars have been shown to discourage pollinators from visiting flowers (Cnaani et al. 2006). Similarly to pollen degradation, nectar dilution can be mitigated through physiological adaptations such as downward-facing flowers (Tadey and Aizen 2001; Aizen 2003). The lower viscosity of diluted nectar is likely to increase the rate at which nectar can be ingested (Harder 1986) but pollinators may risk lowered net energetic gains from visiting flowers with diluted nectar. However, changes in the nectar concentrations of local flower populations may make some flower species more viable to certain pollinators, especially those pollinators associated with more dilute nectars (Pyke and Waser 1981; Baker and Baker 1983). The majority of pollinators do not forage during rainfall (Totland 1994; Poulsen 1996) but investigating changes in pollinator flower choices after rainfall, and whether flower preferences shift, may be a fruitful avenue of research. Additionally, it would be worth identifying which plant species are most susceptible to this nectar dilution from rainfall, what effects nectar dilution has on pollinator behaviour, and which plants and pollinators may be most affected in the future. It has been suggested that dilute nectar can be reproductively advantageous to plants, as it may force pollinators to visit many flowers in order to meet energetic requirements and promote outcrossing in the process (Bolten and Feinsinger 1978). While this need to visit more flowers has been suggested when nectar volumes are reduced (Waddington 1983; Fisogni et al. 2011), flower visits and increased nectar dilutions remain unexplored. However, changes in flower choice

due to nectar preferences are not the only way that pollinator behaviour can be affected.

## Effects on pollinators

### Pollinator behaviour

In general terms, pollinator activity generally decreases during periods of rain, with the rate of flower visitations diminishing as precipitation conditions become more extreme (Totland 1994) and abundance of flying insects decreasing as hours of precipitation increases when measuring all flying insects, including non-pollinators (Poulsen 1996). Adverse weather conditions, which couple rain with higher wind speeds and decreases in temperature, also prevent pollen foraging bees from returning to colonies when compared with returns during good weather (Tuell and Isaacs 2010). Even hive nurses of honeybees *Apis mellifera* which would not be exposed to rain decrease nursing activities during bad weather conditions (Riessberger and Crailsheim 1997). *A. mellifera* are also known to increase foraging activity the day before rainfall (He et al. 2016), but it is unknown if this occurs in other species. Within one study, heavy rains were shown to destroy significant proportions of insect populations (Juillet 1964); however, the effect of heavy rains on insect populations since this study remains unexplored.

However, there are pollinator species which continue to operate during light-to-moderate rain such as bees (Riessberger and Crailsheim 1997; Vicens and Bosch 2000) and bats (Voigt et al. 2011). Hummingbirds continue to forage even during heavy rainfall (Ortega-Jimenez and Dudley 2012b). These differences in behaviour during rainfall affect the numbers of active individuals within an environment, as is seen in the pollinator community composition shift of bee species in blueberry farmland where honeybees dominate during good weather but poor weather conditions cause bumblebees to dominate (Tuell and Isaacs 2010). For pollinators which stay active in the rain, the specific activities they perform can also change, as seen in *A. mellifera* where pollen collection stops during drizzling rain, but nectar foraging continues (Percival 1947). Below we explore the difficulties pollinators face during rainfall events and short- and long-term adaptive responses to these conditions.

Pollinators are known to show peak activity at different times of day (Pierrot and Schlindwein 2003; Baldock et al. 2011), and in some species the timing of this activity is driven by daily patterns of resource output by floral food sources (Stone et al. 1996, 1999), while in others this correlation between activity and resource availability does not appear to be the case (Herrera 2016). In some environments, there are also changes in the daily cycle of precipitation, whereby precipitation has an increased likelihood of

falling at particular times of day (Dai 1999), which could have significant effects on plants and pollinators that have a temporal element to their relationship. This interruption of food supply for foraging pollinators echoes behavioural ecology literature in which interruption in food supplies affects the body mass regulation in birds (Rands and Cuthill 2001). Interruptions caused by rainfall could similarly affect the food stores of hives in eusocial bee species. Computational models which integrate flowering times, peak foraging times and rainfall patterns over the course of a day could help us to understand which plants and pollinators are vulnerable to future shifts in the daily timings of rainfall events.

### Mechanical difficulties of flight during rainfall and physical structures on pollinators

Most pollinators use powered flight to move between flowers, and rainfall has the potential to influence the flight performance of pollinators in a number of ways. Ortega-Jimenez and Dudley (2012a, b) effectively summarised the mechanical penalties for those flying in the rain in a study on the hovering performance of hummingbirds during rain, often using insights from aeronautical studies. These penalties include water load on the surface of the body and wings increasing the overall mass of the flyer; additionally, rain-drop impacts increase downward and backward momentum (Haines and Luers 1983). Aircraft have been shown to experience 2–5% greater drag and 7–29% reductions in lift at rainfall intensities of 100–1000 mm/h; however, due to the difference in scales between aircraft and pollinators, and their different methods of flight, the principles of one will often not apply to the other (Phillips 1989; Dickerson et al. 2012). These factors increase the energetic expenditure that a pollinator needs to use in order to stay airborne. Manoeuvrability and flight control may also be compromised if the distribution of raindrops across the wings and body are non-uniform (Haines and Luers 1983; Ortega-Jimenez and Dudley 2012b), which could affect fine-scale pre-landing movements and may affect pollinators of different sizes in different ways (Dickerson et al. 2012).

These varying mechanical penalties pose different problems to the flight of different species. For instance, as bats are furry they are potentially more at risk to reductions in lift and thrust during flight through wetting of the body (Voigt et al. 2011) compared to hummingbirds which have feathers that are resistant to water penetration (Rijke 1970). Force sensor data suggest hummingbird feathers also appear to dissipate the impact force of raindrops by 50% compared to a flat aluminium rectangle of similar size to a hummingbird wing (Ortega-Jimenez and Dudley 2012b), which may allow hummingbirds to mitigate the effects of rain impacts more so than bats and insects. Hummingbirds also change their body positions during flight in rain. During light-to-moderate rain,



hummingbirds were also observed orientating their bodies and tails to a more vertical position, reducing their impact surface and overall raindrop contact (Ortega-Jimenez and Dudley 2012b). Strangely, however, during heavy rain, hummingbirds orientate their bodies to a more horizontal position (Ortega-Jimenez and Dudley 2012b). Hummingbirds can also shake off water that has collected on their feathers mid-flight to reduce the cost of flying during rain (Ortega-Jimenez and Dudley 2012a).

For insects, which constitute the majority of pollinators and which are considerably smaller than bats and hummingbirds, raindrops pose a greater threat. Despite this threat, few studies have explored insect flight through rainfall, with studies focussed on non-pollinator species. The mechanisms allowing mosquitoes to survive collisions with raindrops have been explored (Dickerson et al. 2012), giving insights into how other pollinators may manage raindrop collision. During heavy rain, impacts with raindrops occur on average every 25 s for mosquitoes (Dickerson et al. 2012) and considering the size of raindrops relative to mosquitoes, and the speed the raindrops fall, it is impressive how mosquitoes survive these periods. Impacts with free-flying mosquitoes were observed using high-speed cameras and a jet of water moving faster than the terminal velocity. Recordings showed that impacts on the wing and legs, which occur the most frequently, cause a roll, pitch or yaw rotation in the mosquito from which they can rapidly recover (Dickerson et al. 2012).

When raindrops directly impact the body of mosquitoes, the impact can cause a rapid downward acceleration of up to 13 body lengths (39 mm) as the mosquito falls with the drop before the two separate (Dickerson et al. 2012). As the mosquitoes are lightweight and the force scales with the size of the insect, the resulting force imparted by the raindrop collision is equivalent to 50–150 times the weight of the mosquito, which the insect can easily survive due to its robust exoskeleton (Gunderson and Schiavone 1989). The sprawled legs of the mosquito then act as a torque which allows them to separate from drops (Dickerson et al. 2012). Despite this survivability, it is worth noting that there is still a considerable risk to the insect when flying close to the ground as collisions can lead to life-threatening impacts or immersion in pools of water (Dickerson et al. 2012).

During these collisions, the mosquitoes and other insects benefit from the hydrophobic nature of their wings which enable water drops to roll off the wing while simultaneously removing dirt (Dickerson et al. 2012). Insect cuticles are also known to have layers of wax and hair which also grant this hydrophobicity (Beament 1961). This is similar to plants whose surfaces exhibit the ‘Lotus-Effect’, whereby the surface structure of the leaf causes water droplets to roll off and remove contaminating particles (Wagner et al. 1996; Byun et al. 2009; Sun et al. 2009; Whitney et al. 2011). Butterfly wings, in particular, are known to have direction dependent

arrangement of nano- and micro-scale structures which confer hydrophobicity and direct water drops away from the body (Zheng et al. 2007).

Alongside these mid-flight collisions, there are potential difficulties if pollinators have accumulated drops of water on their bodies while stationary or gradually during flight, as this would increase the energy needed during take-off and flight. The accumulation of drops of water through fog and dewfall has been explored in mosquitos, where three techniques for water removal were observed (Dickerson and Hu 2014), which may give insights into potential rain-removal behaviours in other species. Within the study, mosquitos were shown to employ a ‘flutter stroke’, whereby the mosquitos use a high-frequency wing beat before take-off to remove the water. A ‘hard landing’ technique was also observed whereby collisions with the ground dislodged water drops (Dickerson and Hu 2014).

It is currently unknown if the mechanisms and behaviours used by mosquitoes are employed by other insects, or if insects can actively dodge raindrops to avoid collisions in light of their sophisticated flight control and range of manoeuvres (Taylor 2001). Although, as the flying speed of most insects is less than the terminal speed of a falling raindrop (Ellington 1991; Dickerson et al. 2014), mid-air dodging may be unlikely. The behaviours and detrimental effects of rain falling from different angles, or in combination with other abiotic conditions such as wind, which have been shown to modify insect flight behaviours (Riley et al. 1999; Ravi et al. 2016), also remain unexplored. Curiously, the estimated sub-optimal mass for an insect in the rain, whereby they face both peak acceleration and applied force from incoming raindrops, closely aligns with bumblebees (Dickerson et al. 2014), which are one of the few insects that continue to forage in light rain (Bruggemann 1958). This begs the question of how bumblebees offset this susceptibility to the applied force of raindrops. Insights into these particular problems may not just increase our understanding of insect flight, but also benefit and inspire the design and implementation of micro-aerial vehicles (Dickerson et al. 2014).

## Energetics of flight during rainfall

These mechanical penalties of flying during rain all contribute to a decrease in flight efficiency, making flight during rain more energetically costly. These energetic costs are coupled with other energy-related problems, such as thermoregulatory expense, which has the potential to lower the net energy gained. In order to maintain a normal body temperature, bats exhibit a higher flight metabolism when their fur is wet (Voigt et al. 2011). In some species, this additional cost almost doubles the total flight cost compared to the same bat flying in dry conditions (Speakman et al.

2003). With this increased flight metabolism in mind, it is unsurprising that bats reduce or completely stop foraging activities during rainfall (Voigt et al. 2011). These energy costs are minimised in pollinating birds due to the hydrophobic nature of their feathers and the effective insulation that their feathers provide (Rijke 1970; Dawson et al. 1999; Ortega-Jimenez and Dudley 2012b).

These thermoregulatory costs can also be applied to insects, for instance, a wet body would also raise the costs of heating the body to the temperature required for flight in pollinators such as bumblebees (Heinrich 1975, 2004), as seen in *Bombus* sp. which needed thoracic temperatures above 30 °C for sustained flight (Krogh and Zeuthen 1941). Flowers can offset these losses to pollinator temperature through heat rewards, whereby the heat of flowers is transferred to the pollinator (Kevan 1975; Rands and Whitney 2008; Whitney et al. 2008; Harrap et al. 2017), although rain could also lower the temperature of a flower, lessening these heat rewards.

### Rain avoidance

To avoid these energetic costs, many pollinators have evolved methods of detecting changes in weather conditions, allowing for weather forecasting and rain avoidance. The primary method of rain detection, other than direct contact, appears to be the detection of changes in barometric pressure. Clear weather and moderately strong winds are generally associated with a rise in atmospheric pressure, whereas severe weather conditions (such as rainstorms and high winds) are associated with a drop in pressure (Dunlop 2003; Pellegrino et al. 2013). Many insect species have demonstrated behavioural changes during barometric pressure shifts (Wellington 1946; Marchand and McNeil 2000; Cabrera Walsh et al. 2008). One study showed that three taxonomically unrelated insect species, differing in mass, morphology and seasonal biology, adjusted their behaviour in response to changes in barometric pressure (Pellegrino et al. 2013). These changes, which generally entail a decrease in activity, especially those occurring under decreasing pressure, are considered to reduce the probability of injury or death under adverse weather conditions (Pellegrino et al. 2013).

Little is known about how these barometric pressure changes are detected by insects. However, it is possible that these changes relate to hair-like mechanoreceptors which are deflected by faint air currents or hygroreceptors, where changes in the geometry of the cuticular wall lead to dendritic action (Keil 1997; Tichy and Kallina 2010; Pellegrino et al. 2013). More experiments which observe the behaviour of taxonomically unrelated species during variability in barometric pressure would be beneficial to develop general theories, as would work which focusses on pollinator species.

### Rain as environmental noise

The behaviour of pollinators changes constantly as they react to and navigate around their environment. Their behaviour could be affected if their perception and sensory intake is altered by rainfall, as rain could potentially obscure visual aspects, both at a distance and at smaller scales. Rain could also obfuscate olfactory signals through direct removal of scent on flowers, removal of volatiles from the atmosphere (Starr and Mason 1966) and through environmental noise as rain is known to affect the emission and ratios of volatile organic compounds (Helmig et al. 1998; Wilson et al. 2015; Lawson et al. 2017a). Similarly, rain may wash away olfactory signals deposited by social pollinators that might be used by later visitors to inform their action on the flower (Goulson et al. 1998; Reader et al. 2005; Pearce et al. 2017). Other sensory modalities that mediate the interactions between pollinators and flowering plants may be compromised during and after rain, such as the electrostatic nature of flowers (Vaknin et al. 2001; Clarke et al. 2013), their temperature patterns (Dyer et al. 2006; Whitney et al. 2008; Harrap et al. 2017), scent patterns (Lawson et al. 2018) and surface textures (Kevan and Lane 1985). If these modalities are affected, the multimodal interactions between these signals could also be changed significantly (Leonard et al. 2011; Kaczorowski et al. 2012; Leonard and Masek 2014; Lawson et al. 2017b).

### Summary

The effect of rain on pollination involves multiple complex interactions at various scales both microscopic and macroscopic. These effects permeate many facets of the plant–pollinator relationship, including phenology, physiology, animal behaviour and energetics. This review presents gaps in our current knowledge of the relationship between rain and pollination while highlighting areas which would benefit from future research. Many of these knowledge gaps relate to the susceptibility of certain species to outcomes of rainfall contact and how this will affect pollinator choices and behaviour, such as damage to flowers, nectar dilutions and the different ways floral signals can be compromised. Although some may be broad in scope, and difficult to implement, there are examples which could be investigated with simple experimental techniques. On a wider scale, it would be valuable to understand how the structure of plant–pollinator community's networks is affected by increases in rainfall patterns and to measure the robustness of networks faced with these effects.

By taking a deeper look into the relationship between abiotic factors like rain and the interactions between flowering plants and their visitors, we will gain a better

understanding of pollination ecology as a whole. Insights into how these relationships might be affected as the environment undergoes anthropogenic change may help us understand and mitigate the economic and ecological consequences we may face in the future. This is an extensive and complex subject area, but it is our hope that despite the intricacy of the subject, this review motivates and inspires new research exploring this rich plant–pollinator interplay. There is still much to be understood and there are many other areas within the subject of pollination ecology that remain underexplored (Mayer et al. 2011) but considering the dynamic and interdisciplinary nature of this research area, and the talented researchers that work within it, the possibilities for future discovery are exciting.

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